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FACTORS CONTROLLING THE DISTRIBUTION OF FOREST TYPES, PART II

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Determination of Factors Limiting the Distribution of Forest Types

The first phase of this study dealt with the measurement of soil and climatic factors in each forest type. The second phase seeks to apply the results in explaining the presence or absence on different sites of various tree species indigenous to the region, and then to determine the limiting factors in the distribution of each species and forest type. A more direct way would be to grow the trees under controlled conditions, but in view of the long life period of trees and their demands upon space, the physical difficulties in the way of such an undertaking render it desirable first to collect all the information available from a study of natural conditions.

A number of difficulties in the method adopted become at once apparent. One of these is that after measuring the factors on the sites where a certain species thrives and on other sites where it does not occur, we can not always be absolutely sure that its absence on the latter sites is not due to non-introduction, or to competition with other species rather than to adverse factors in the habitat itself. In the case of widely separated habitats these questions may become serious ones, but when the study is confined to one locality they can usually be disposed of. The question of introduction is at once eliminated. Opportunities are usually found for securing evidence as to whether or not competition is an important factor. In order further to eliminate the possibility of error, the study of natural distribution has been supplemented by planting a number of species in habitats where they do not occur naturally.

The greatest problem arises from the fact that the transition from one site to another involves changes in several physical factors. The question then to be decided is, which factor is the limiting one? Usually a general knowledge of the occurrence and requirements of the species will aid in arriving at a decision, but in some cases direct experimental data are required. The planting experiments just mentioned will throw considerable light on the subject. If the planting fails, the appearance of the plants will often furnish a clue to the cause of their death. If the plants grow on a site where the species does not occur naturally, it may indicate failure of seed to have reached the site in question by natural methods, or circumstances adverse to germination and early establishment of seedlings, or possibly inability to compete successfully; or it may indicate that climatic conditions for the period of the experiment have been unusually favorable and that therefore success is only temporary.

Change of site in this region usually means a change in altitude or slope exposure. In either case the physical factors mainly concerned are temperature and moisture. Soil appears to be important in this region only in so far as it affects available moisture supply. From this standpoint it is very important and undoubtedly deserves more attention than it has received in this study. Light is determined mainly by density of cover and is therefore under control for experimental purposes.[12]

There is a certain well defined relation between temperature and moisture conditions which, with a few local exceptions, holds for all the forest types. An increase in elevation or change to northerly aspect is accompanied by falling temperature and rising soil and atmospheric moisture, while the opposite changes in altitude or aspect are accompanied by rising temperature and decreasing moisture. The changes in both temperature and moisture manifest themselves in several ways. A change in seasonal temperature involves first a change in the quantity of heat energy available for carrying on plant activities, and secondly in the duration of the growing season as determined by the period in which effective growing temperatures occur and the absence of frosts and snow. Moisture supply is determined by precipitation, by storage in the soil in a form available for plant use, and by evaporation. The last named factor is in turn determined by temperature, wind and relative humidity. Temperature is most important not only in determining the rate of evaporation, but also, by controlling the rate of melting of snow, greatly affects the absorbtive capacity of the soil. The effect of temperature

[12] [Is it not possible that with the differences in elevation involved in this study there may be sufficient differences in the intensity of solar radiation to play an important part? It may be, however, that the increase in solar radiation with altitude is largely masked by the increase in the moisture vapor of the air at the higher elevations. —EDITOR.]

upon the melting of snow is of tremendous importance in regulating growing conditions in this region. The abundance of moisture which makes possible the luxuriant spruce forests, for instance, is due not so much to high precipitation as to the fact that the winter precipitation comes mainly in the form of snow which lies on the ground until well into the month of June. By the time the snow is gone, the soil is saturated and summer temperatures are at hand. The result is immediate growth and a maximum utilization of moisture. In the yellow pine type, on the other hand, the snow usually disappears by April, but active growing temperatures seldom come until after May 15. The result is that most of the moisture in the upper foot of soil is evaporated before plants can use it.[13] From the foregoing it becomes obvious that temperature and moisture as factors controlling plant growth are almost inseparable in nature, and that although the direct effect of moisture is more obvious, temperature is really the dominant factor because it virtually controls moisture.

The temperature data employed in this study are air temperatures. It is generally recognized that air temperature is but a rough expression of the heat energy absorbed and utilized by the plant. It is also evident that measurements of total solar radiation would not give the results desired by plant physiologists. The writer has approached the problem in a preliminary way by measuring transpiration in potted tree seedlings, but the work has not been carried sufficiently to warrant definite conclusions as to its practicability.

On the basis of existing knowledge regarding the natural occurrence of various tree species in this region, the tentative conclusion has been formed that the upper altitudinal range of all species is determined by low temperature and the lower range by deficiency in moisture. In other words a species belonging to a given forest type, on descending into the next lower type is arrested not by the higher temperature prevailing there, but by the deficiency in moisture; on the other hand, on ascending into altitudes above its natural habitat, it encounters unfavorable conditions not in the increased moisture supply but in the lowered heat supply. This hypothesis agrees with the findings of Shreve[14] in the Santa Catalina Mountains of southern Arizona, but is contrary to the conclusions of Bates[15] whose studies in the central Rocky Mountains point to low winter temperature of the soils as the upper control, and high air temperature as the lower control.

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[13] [Although the melting snows penetrate deeply into the less pervious soils of the open areas known as "parks," the summer rains apparently do not, and it is probable that the porosity of the different soils—both on account of moisture and soil aëration—is important in determining whether or not trees will succeed.—EDITOR.]

[14] Shreve, Forrest. "The Vegetation of a Desert Mountain Range as Conditioned by Climatic Factors," Carnegie Inst. of Washington, Publ. 317, 1917.

[15] Bates, C. G. "Forest Types of the Central Rocky Mountains" (to be published by the U. S. Weather Bureau).

In order to proceed intelligently with a discussion of this subject, it is necessary to define our conception of temperature and moisture in their relation to the problem at hand. By temperature is meant the heat supply as determined by solar radiation and air temperature, and imperfectly expressed by the temperature of the air and soil. By moisture is meant the balance between moisture supply and consumption which might be expressed by the ratio between available soil moisture and transpiration.

The aspects of temperature with which we are primarily concerned are its availability as a source of energy for photosynthesis and transpiration, its relation to absorption and other vital processes, and injurious effects due to excessively high temperature.

The ability of a plant to carry on photosynthesis and assimilation with a low heat supply is believed to be the dominant factor in deciding whether or not it can exist in the high altitudes of this region. That plants differ widely in their heat requirements is a matter of common observation. For example a number of herbaceous plants commonly blossom before the snow is entirely gone while others show no signs of activity whatever.

Transpiration need be considered here only when it occurs in excess. Under this condition temperature transforms itself into a moisture factor, and to that extent the effects of temperature and moisture are inseparable. The relation is further complicated by the fact that in this region an increase in temperature is always accompanied by a decrease in precipitation as well as by an increase in evaporation; and a decrease in temperature is accompanied by an increase in precipitation and a decrease in evaporation. Therefore when moisture deficiency is cited as the limiting factor in the downward extension of a species, it must be recognized that we are dealing not only with deficient moisture supply resulting from low percipitation, but also with excessive water consumption due mainly to high temperature.

Injuries from overheating are closely related to and often indistinguishable from drought injury. It may be assumed that transpiration, by its cooling effect, tends to prevent the occurrence of excessive temperature within the plant tissues, and therefore it is quite probable that within certain limits an increase of water supply sufficient to maintain the maximum transpiration rate will mitigate the injurious effects of high temperature. It is known that certain species, such as the western yellow pine, the junipers, and Arizona cypress are capable of withstanding much higher atmospheric temperatures than prevail in their native habitats, providing that they are well watered. Arizona cypress in particular has shown itself remarkably adaptable in this respect. This tree normally grows in the mountains where maximum temperatures rarely exceed 95 degrees F., but under irrigation it thrives in localities where maximum temperatures rise to 120 degrees F. On the other hand, species like Engelmann spruce and Douglas fir appear to have decided limitations in regard to endurance of high temperature.

We have seen from the preceding discussion that when the downward extension of a tree is attributed to deficient moisture we are also dealing with high temperature, and therefore strictly speaking moisture alone can not be regarded as the limiting factor. Moreover, beyond certain temperature limits heat regardless of moisture may be the limiting factor. What we are concerned with in this study, however, is the actual rather than the ultimate barrier. If, after eliminating other conditions, we find that a plant has all the moisture it can use and still fails, we may assume that it has encountered its limitation in heat conditions. If, on the other hand, the moisture supply is known to be near the minimum and the temperature well within the limits for the species, it may be concluded that moisture is the limiting factor. The following practical test has been applied in this study. When a species is transplanted below its natural range into a hotter and drier climate, if it succumbs under natural conditions but thrives when the moisture supply is increased by cultivation or watering, lack of moisture is regarded as the condition responsible for the failure of the species to descend below its present range.

In the following pages the range of each of the coniferous species of this locality will be discussed from the standpoint of limiting factors.

PINON-JUNIPER TYPE.—The pinon (*Pinus edulis*), two junipers (*J. utahensis* and *J. monosperma*), and a third juniper (*J. pachyphloca*) which is of limited occurrence, form a woodland belt representing the transition from desert to timber forest. Their characteristic low form and open stand adapt them to the arid conditions of this type. All the evidence at hand points to deficient moisture as the factor limiting their encroachment upon the desert, and low temperature as the factor checking their ascent into the yellow pine type where moisture conditions are more favorable for vegetation in general. The woodland is approached from the east in this region along the Santa Fe Railroad west of Winslow, on a very gradual ascent. The first suggestion of an approaching forest is indicated at about 5,000 feet elevation by straggling junipers scarcely more than a foot high. Four or five miles farther on the junipers become distinctly more prominent in both numbers and development but continue to be undersized. Normal development is attained at an elevation of a little over 6,000 feet. The pinon makes its appearance at a somewhat higher altitude than the junipers. At about 6,500 feet, both the junipers and the pinon have attained their maximum development. Here the western yellow pine (*P. ponderosa scopulorum*) becomes conspicuous as a low bushy tree. Ascending to 6,700 feet the yellow pine increases in size and numbers, while the pinon and the junipers become less abundant, though still maintaining good size. At this point the alligator juniper (*J. pachyphloea*) makes its appearance. It persists well up into the yellow pine type, thus indicating a higher moisture and lower temperature requirement than the other two members of the genus. The mean annual rainfall at the lower and upper limits of the pinon-juniper type are about 10 and 18 inches respectively. Of hardly less importance is the depth of the soil. At the lower limits in certain localities, bedrock is encountered within 2 or 3 inches of the surface while at the upper limit it is 2 or more feet below. In this case both precipitation and depth of soil increase the moisture supply in the higher altitudes. Farther east toward Winslow the soil becomes deep, but precipitation decreases, and here the trees are absent. On the western slopes of the Colorado Plateau the lower limits of the pinon-juniper are less distinct owing to a more varied topography.

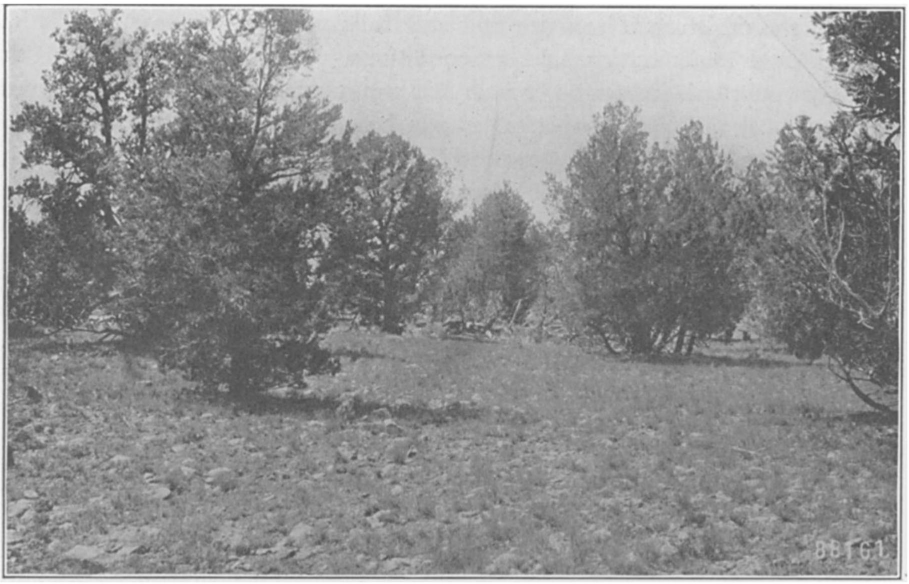

FIG. 9. Pinon-juniper type, showing open character and form of trees.

That lack of moisture rather than excessive heat or unfavorable soil composition prevents the growth of the woodland species in low altitudes is shown by the fact that sizeable specimens occur along water courses well below the general limits of the woodland. The fact that these trees respond to cultivation and irrigation by greatly increased growth is ample evidence that the higher soil moisture of the yellow pine type is not unfavorable to them. Nor is competition a limiting factor because there are any number of openings in the yellow pine forest where they would encounter neither root nor crown competition. Moreover the junipers commonly reproduce in the shade of older trees in their natural habitat. There is abundant evidence, however, that low temperature, through its effect on photosynthetic activity, is the limiting factor. Wherever a pinon or a juniper occurs above the middle altitudes of the yellow pine type, it is invariably on a southerly exposure. The same observation has been made by Robbins[16] in Colorado. Fairly large specimens have been observed in sunny, protected situations as high as 7,300 feet. Pinons grown from seed and later field planted in the vicinity of the Fort Valley Experiment Station still persist after five years, but are not thrifty.

YELLOW PINE TYPE.—Western Yellow Pine (*Pinus ponderosa scopulorum*) occurs in pure or almost pure stands throughout the type. In fact it dominates so completely that the few associated species are seldom mentioned as being a part of the stand. At the upper and lower extremes of its range it exhibits much the same characteristics as the woodland species. Isolated specimens occurring in the pinon-juniper type, though sometimes of large diameter and apparently several hundred years old, are usually of low stature unless found along a water course, in which case they reach fairly good height. Planted trees far below the natural range make a tremendous height growth under irrigation, but without irrigation or cultivation they almost invariably die during the first or second season. In its extreme upper range it is confined to southerly exposures. Specimens observed in such situations are

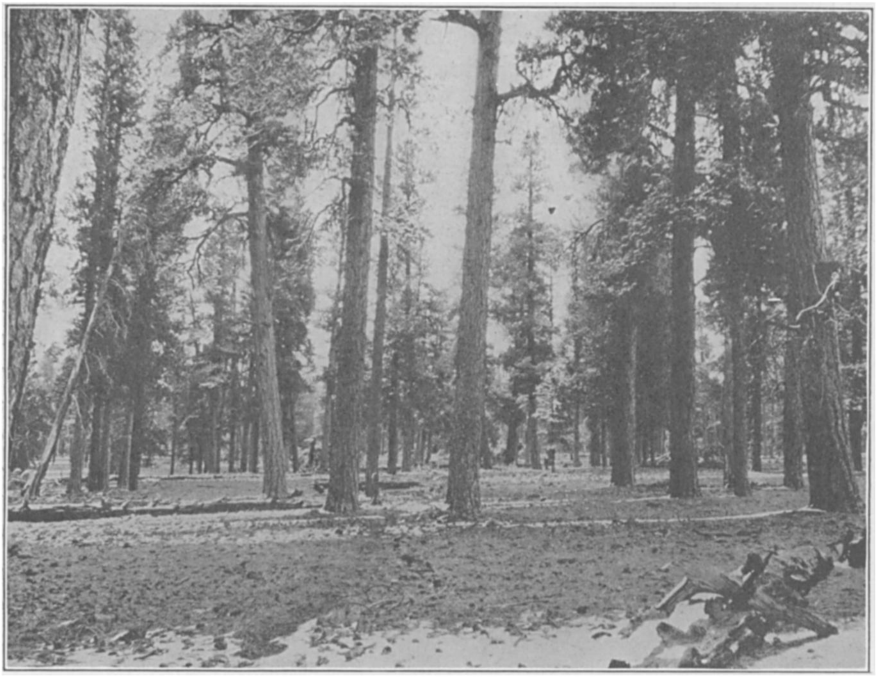

FIG. 10. Yellow pine type. Meteorological station in the background.

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[16] Robbins, Wilfred W. "Native Vegetation and Climate of Colorado in their Relation to Agriculture," Colo. Agr. College, Bul. 224, 1917.

sometimes of good size but produce few cones. This condition was conspicuous in 1918 which was an exceptionally good seed year in the yellow pine type. Plantings were made in 1918 in all the forest types above the pinon-juniper up to the Engelmann spruce type. In every case the survival to date is fairly good, and, excepting in the Engelmann spruce type, fairly good height growth has resulted. A noticeable feature, however, is that in the Engelmann spruce type the length of the needles formed during 1918 was below normal. On a north slope in the spruce type, yellow pine plants placed in a small opening where they received about 5 hours of direct sunlight per day during June, July, and August scarcely more than opened their buds, and developed only mere rudiments of needles. On a southerly exposure nearby, in a larger opening receiving practically full sunlight during June, July, and August height growth was almost equal to that in the yellow pine type, but the needles were decidedly below normal length. Seed sown in a well prepared bed in this opening showed only 6 percent germination, while seed from the same lot sown in the yellow pine type gave 67 percent. Seed of Engelmann spruce and bristle-cone pine sown in the above opening gave practically the same germination as in the greenhouse under a mean temperature of about 70 degrees F. It is interesting in this connection to note that hardy root crops, such as carrots and turnips, did not mature. The vegetative growth was decidedly below normal height, though of rich green color. Beans grow only 3 or 4 inches tall, had poorly developed leaves, and did not blossom, although they remained uninjured by frost until September 17 and were not killed until October 17. In the yellow pine type 3,200 feet lower beans made a luxuriant growth and fruited freely up to August 17, when they were severely injured by frost and were finally killed by frost on September 17. From the foregoing examples it becomes evident that, although the frostless season was some 30 days[17] longer in the Engelmann spruce type, the temperature was too low for yellow pine. As has been previously pointed out, the extreme minimum temperatures are usually lower in the yellow pine type than in the Engelmann spruce type. The vital temperature deficiency in the Engelmann spruce type with reference to growth of yellow pine lies in the low maxima. In other words, effective temperatures for plants of medium to high heat requirements are seldom reached or are of too short duration for good growth. This is illustrated by the record of maximum temperature and the total number of hours with temperature above 70 degrees F., as shown in the following table and in figure 3, Part I.

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[17] Table 6 in part I shows a difference of only 8 days in the 1918 frostless period. This table, however, is based upon temperatures of 32° or below. Tender plants are often frosted when the temperature recorded in a standard Weather Bureau shelter is one or two degrees above 32° F.

Forest type	Mean maximum temperature (1918), Degrees F.					Total No. hours 70° and Above (1918)
	May	June	July	Aug.	Sept.	
Yellow pine type (Fort Valley)	60.2	79.8	75.1	73.8	72.3	633
Eng. spruce type, NW slope, cover	45.6	62.3	59.0	57.9	54.0	4
Sw slope, open[18]	48.0	65.0	60.7	59.7	59.2	70[18]

Soil temperature is a further index of the heat supply. Comparable records are available at all the stations only for the period July–September, but these are sufficient to indicate a great difference in the heat available during the growing season. Heat supply during the growing season is directly related to the ability of the plant to carry on photosynthesis. What may be of equal importance is the period during the winter months when the soil remains frozen, or at a temperature so low that the moisture can not be absorbed by roots. On northerly exposures in the Engelmann spruce type the soil temperature is continually below 32 degrees F. from about December 1 to June 1, while in the yellow pine type the period is much shorter, usually not over 60 to 90 days. The presence of salts in the soil water tends to lower the freezing point; how low the temperature can fall without freezing the soil water depends upon the strength of the solution. Observations by Sampson at the Great Basin Experiment Station in Utah and by the writer at the Fort Valley Experiment Station indicate that the soil does not ordinarily freeze until a temperature of 30 to 31 degrees F. is reached. According to investigations by Kihlman,[19] the soil moisture ceases to become available to plants at a temperature of 1° C. (1.8° F.) above the normal freezing point.

A casual experiment during the winter of 1918–19 throws considerable light on this question. Four 4-year-old yellow pines and one 5-year-old bristle-cone pine used for transpiration experiments in the Engelmann spruce type were stored in a log cabin over winter. All the plants were in 4-inch sealed iron pots. The available moisture supply was kept at about 8 percent by occasional fillings. Early in May, 1919, an examination revealed that all of the yellow pines were dead, while the bristle-cone pine was in perfect condition. A weighing of the pots at this time showed the soil to be up to the standard moisture content. The only apparent explanation for the results is that the pots were frozen solid from December 1 to May 1 and thus no moisture was available to the roots. During this period transpiration, slight as it was, was sufficient to kill the yellow pines. The bristle-cone pine, however, because of greater resistance to transpiration, or because of greater endurance of desiccation, was uninjured. Yellow pine, bristle-cone pine, limber pine, Douglas fir and Engelmann spruce planted in the soil under natural conditions outside the cabin where they were covered through the entire winter by several feet of snow lived through in good condition excepting that 3 out of the 5 yellow pines and a smaller percentage of Douglas fir and Engelmann spruce had dead terminals. It is quite probable that the injury to the terminals occurred before the first heavy snowfall when the soil was frozen but the snow was not deep enough to cover the plants completely. These observations indicate that yellow pine is more subject to winter killing than is limber pine or bristle-cone pine.

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[18] Interpolated in part.

[19] Kihlman, A. Osw. "Pflanzenbiologische Studien aus Russich Lapland." Acta. Soc. pro Fauna et Flora fennica. 6: 1–263, 1890.

Sachs found that cooling the soil to a point slightly above freezing slowed down the water absorption of *Phaseolus, Nicotiana,* and *Cucurbita* until wilting occurred. Kihlman confirmed Sach's results, using *Cucurbita pepo,* 3 pots of which were packed in ice, with a control pot in sawdust. When the soil in the ice-packed pots dropped to 1° C. the three turgescent plants were exposed to the sun and wind at a 12° C. air temperature. Two hours later the plants in the ice-packed pots were all wilted. The soil in one of these was then warmed to 25–28° within 15 minutes by adding lukewarm water, and kept at this temperature. In spite of increasing air temperature and wind velocity, the plants had almost recovered their turgidity within four hours. Adding 10–12° water to another pot produced a slow change, but turgidity was restored by the following morning. A third pot was left longer on ice, the plant in consequence showing greater injury, the cotyledons never wholly recovering turgidity. No mention is made of the control pot; apparently these plants did not wilt. (From abstract by E. C. Rogers.)

The following table gives a comparison of soil temperatures within and above the natural range of yellow pine.

	Altitude	Aspect	Cover	Soil Temp. 12" July–Sept., 1918, degrees F.	No. of days with soil temp. 32° F. or lower winter 1917–18, depth	
					12"	24"
Yellow pine type........	7,300	Level	Open	65		
		"	Partial cover	59	48	10
		"	Dense cover	57		
Douglas fir type........						
Last yellow pine....	8,900	South	Open	57		
No yellow pine.....	8.900	NW	Partial cover	51	58	20
" " "	10,000	South	Open	55		
Engelmann spruce......						
Open..............	10,500	SW	Open	52		
Cover.............	10,500	NW	Dense	45	182	156

Transpiration furnishes a more direct comparison of the relative amounts of heat utilized. Two series of 3-year-old plants (A containing 6, and B 3 plants) were run during a period of six weeks, from August 21 to September 30. Both series were exposed to open air conditions at the Fort Valley Experiment Station from August 21 to September 19. On September 20 Series B was taken to the Engelmann spruce type and placed in an opening where the plants were exposed to practically full sunlight. The results follow:

	Mean daily transpiration per plant, gr.		
	Aug. 21–Sept. 19	Sept. 21–30	Decrease second period
Series A (in Y. P. type continually)	3.83	3.63	5%
Series B (in spruce type Sept. 21–30)	4.36	3.00	31%

The above figures indicate a reduction of the transpiration rate by 26 percent as a result of moving the plants to the Engelmann spruce type. Although the study has not been carried far enough to determine the relative effects of different factors our knowledge of the conditions suggests temperature as playing the leading rôle.

Data now at hand show quite conclusively that yellow pine will not thrive in temperatures as low as those encountered in the Engelmann spruce type, unless it be in the extreme lower portions. The indications are that the possible extreme upper range of the species conforms closely to its present occurrence. This is being checked by two planting and instrument stations between the uppermost yellow pine and the Engelmann spruce type.

DOUGLAS FIR TYPE.—Unlike yellow pine, Douglas Fir (*Pseudotsuga taxifolia*) occupies the sites most free from rigorous climatic conditions. The temperature, though low (mean annual for 1917 and 1917 41.7° F.) is characterized by great moderation. Frosts are of rare occurrence during the growing season. The frostless period is almost as long as in the pinon-juniper type 3,000 feet lower. Precipitation is practically equal to that of the Engelmann spruce type, and soil moisture is sufficient for all but the plants of distinctly high moisture requirements. Our knowledge of the characteristics of Douglas fir indicates that its occupation of these favorable sites is dictated by the requirements of the species.

Frost damage is one of the commonest difficulties encountered when Douglas fir is taken outside its natural habitat. In nursery culture sensitiveness to frost is always a factor to reckon with in the Rocky Mountain region. Much the same difficulty is experienced in the eastern states. The species has been extensively introduced in Europe where frost injury is recognized as one of the main difficulties in its propagation. Douglas fir seedlings respond very quickly to the first warm days of spring. The tender shoots are later killed by frosts which are apt to occur late in May or early June. It is therefore not mere coincidence that this species occupies the climatic zone which in this region is least subject to unseasonable frost.

Douglas fir is also subject to winter killing. According to available information the damage takes place during temporary periods of sunny weather in the winter time when the soil is frozen. At such times the transpiration becomes active but soil moisture is not available to the roots. Douglas fir plants grown in nurseries in the yellow pine type almost invariably winter kill unless the tops are covered. Yellow pine in the same nurseries is rarely injured. In their native habitat Douglas fir seedlings are covered by snow throughout the winter and early spring. They are also shaded by the aspen in whose shelter they commonly grow.

Another peculiarity of Douglas fir is that the tops frequently dry up when exposed to strong sunlight, even when the soil has a fairly high available water content. For this reason seedlings and transplants grown in nurseries must be shaded. Douglas fir plantations suffer severely in open spots, while adjoining aspen-covered plots are uninjured. Whether the injury is due to superheating of the tissues or to disturbance of the proper balance between water loss and water absorption is more or less of an open question. Obviously the maintenance of a vigorous transpiration stream would tend to prevent superheating; on the other hand, it is conceivable that a plant may be so constituted that even though the water supply at the roots is at an optimum, it can not maintain transpiration at a rate sufficiently high to prevent excessive leaf temperatures. Douglas fir apparently has distinct limitations in this respect, but whether its absence in the yellow pine type or even in the pinon-juniper type is accounted for by high temperature rather than low moisture supply is doubtful. The question can be answered by the simple experiment of planting a few Douglas firs in the lower types under conditions where they will have all the water they can utilize. In this connection, mention may be made of the fact that in transpiration experiments carried on last summer in the yellow pine type, Douglas fir and Engelmann spruce seedlings grown in pots where the available moisture content of the soil was not allowed to fall below about 8 percent, no evidence of injury was discernible. In the greenhouse, however, the leaves on some of the Douglas fir plants were injured when the temperature was allowed to rise to 100° F., while the Engelmann spruce alongside was uninjured.

Since frost, winter killing, and exposure to direct sunlight are most injurious in altitudes below the Douglas fir type, the question arises whether they, rather than merely a lack of soil moisture, may not account for limiting the downward extension of the species. It is known that the injuries described largely disappear after the seedling stage is passed. It is also known that artificially established Douglas fir seedlings thrive in the shelter of groups of yellow pine when given winter protection and water. It is reasonable to assume, therefore, that if soil moisture in the yellow pine type were adequate to support Douglas fir, the latter would struggle through the seedling stage by taking advantage of the protection afforded by groups of living trees and particularly of fallen trees. Its tolerance of shade would make this possible. As a matter of fact, this does happen in the upper portion of the type where moisture more nearly meets the requirements of Douglas fir. But this expedient is not sufficient to enable it to migrate far into the lower altitudes because deficient soil moisture together with high transpiration becomes a more and more unsurmountable obstacle.

Frost, winter killing, and injury from exposure to direct sunlight are far less active in checking the upward than the downward extension of Douglas fir. In the Engelmann spruce type, for example, frosts are but little more prevalent than in the Douglas fir type, and the range of temperature is far less. An equal or greater amount of protection is afforded by snow, underbrush, aspen and down timber. The remaining factor to be accounted for is heat.

The mean annual temperatures in the Douglas fir and Engelmann spruce types for the years 1917–1918 were 41.7° and 36.0° respectively (Table 1 in Part I). During the growing season, June to September, inclusive, the mean maxima were 67.1° and 58.2° respectively, and the total number of hours with temperature 70° or above, 169 and 2½ respectively (Table 8 in Part I). Douglas fir has been planted at the base stations in both forest types and at two intermediate stations. The plants are thrifty excepting at the Engelmann spruce base station on a northwest slope, where they have made but little growth. Present indications are that the heat supply in the Engelmann spruce type is deficient for Douglas fir.

Limber Pine.—Limber pine (*Pinus flexilis*) is associated with Douglas fir almost throughout the range of the latter; but limber pine is able to occupy wind-swept slopes and ridges where Douglas fir will not grow. Its ability to withstand strong insolation accompanied by high wind on steep southerly slopes at high altitudes is noteworthy. Special studies have been made on one such slope which ranges in elevation from about 9,300 to about 10,000 feet. During the growing season of 1918, the soil moisture on this slope ran slightly below that in the yellow pine type. The same was true of maximum air temperatures and mean soil temperatures. Wind movement was practically three times as high as in the yellow pine type. On the lower ⅔ of this slope limber pine is the only tree, and here it occurs only as scattered individuals. Near the top of the slope it begins to give way to bristle-cone pine (*Pinus aristata*) while across the ridge on a northerly aspect it is largely supplanted by Engelmann spruce. The evidence indicates that the upper limit of limber pine on this slope is determined by low temperature during the growing season. This point is, however, being checked by plantations in the Engelmann spruce type. The extreme lower range of the species in this locality extends well into the yellow pine type where its occurrence is limited to north slopes and canyon bottoms. Attempts to transplant the tree to the yellow pine type below its natural occurrence have failed excepting in 1918 when moisture conditions during the growing season were above normal. In the greenhouse where well watered, it has withstood a temperature of 100° F. without injury. These experiences indicate that the lower range is determined by deficient soil moisture rather than by high temperature.

ENGELMANN SPRUCE TYPE.—*Engelmann Spruce.*—Engelmann spruce (*Picea engelmanni*) exhibits a sensitiveness to frost, winter killing and strong sunlight similar to though less pronounced than that of Douglas fir. Throughout its range it avoids dry, sunny sites, particularly those exposed to high wind. The Engelmann spruce type, though having a shorter frostless period than the Douglas fir type, is generally free from frost during the growth season. The temperature rarely rises to the 70 degree mark, and is exceedingly constant; on typical spruce sites the daily range is seldom over 20° F. The deep snow cover between about December 1 and the middle of June renders frost and winter killing relatively harmless to reproduction. When the snow disappears, the danger of killing frost is practically past. Autumn frosts approach so gradually as seldom to cause damage to woody plants.

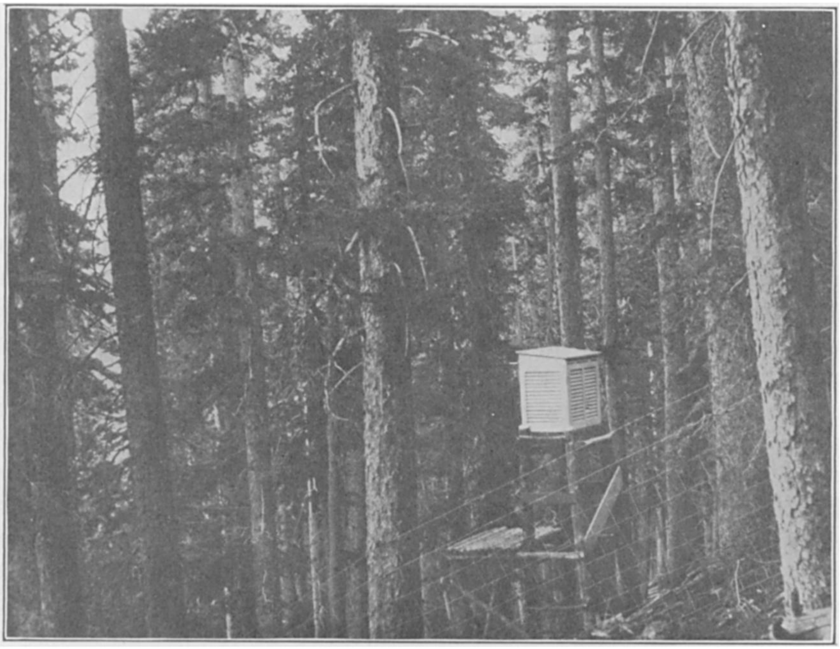

FIG. 11. Meteorological station in a mature forest of Engelmann spruce and cork-bark fir on a steep north slipe at 10,500 feet.

Engelmann spruce, like Douglas fir, appears to avoid high temperatures. Undoubtedly the injurious effects of excessive heat can, to a certain extent, be overcome by increasing the water supply; but observations indicate that this species as well as the Douglas fir has pronounced limitations in this respect.

Attempts to establish Engelmann spruce in the yellow pine type by planting have been, on the whole, unsuccessful. Some plants have survived two seasons, but their present appearance predicts failure. Shading and irrigation are beneficial especially when the two are combined.

The behavior of the spruce in the Douglas fir type is illustrated by the following experience. In 1912 a seedbed of Engelmann spruce was established in the shade of Douglas fir trees at 8,700 feet. An excellent stand of seedlings resulted. They received no water other than natural precipitation, but were covered during the winter. After two years it was evident that the plants were not growing as rapidly as they should, and therefore the bed was heavily thinned, with slightly beneficial results. At the age of three years a number of seedlings were transplanted into a more open situation in the shade of aspen. Winter protection continued, but the seedlings were not watered. At the end of five years it was evident that the plants were distinctly below normal size and in the sixth year they died. Throughout the entire course of the experiment there was no evidence of violent injury such as results from frost winter killing or too intense solar radiation. The conclusion therefore is that the plants suffered from deficient soil moisture combined with excessive transpiration.[20] In view of the fact that the precipitation in the Douglas fir type is practically the same as in the Engelmann spruce type, and there is no important difference in soil, differences in moisture conditions must be attributed to factors affecting transpiration and direct evaporation from the soil. Of these factors, temperature is undoubtedly the most important in this case. It should be noted, however, that the unfavorable action of high temperature is not direct, but indirect, through its influence upon moisture. As stated in the discussion of Douglas fir, Engelmann spruce has been observed to withstand temperatures of 100° F. when supplied with abundant moisture.

Engelmann spruce reaches its upper limit at timber line which in this study has been taken as marking the lower boundary of the alpine type. Timber line is here regarded as the line at which the trees cease to have the erect tree-like form. Both Engelmann spruce and bristle-cone pine persist in the bushy or trailing form several hundred feet above this point. Mean air temperature at the timber line station is only from 4 to 5 degrees lower than on the optimum spruce sites, while the mean maximum is but 3 degrees lower. The spruce bears fertile cones right up to the point where it becomes trailing. One specimen was found bearing cones about 300 feet above this point but since this observation was made after the time of seed dispersal, it is not known whether the seeds were fertile. Both spruce and bristle-cone pine, however, reproduce well at timber line. Saplings grow erect and with apparent vigor until they attain a height of 6 or 7 feet, above which the tops are killed back. This gives rise to the theory that the injury takes place in the winter time when everything below 6 or 7 feet is covered with snow. The dead terminals are frequently barked, which points to strong abrasive action resulting from the snow and sleet being driven against the stems by high winds. Sleet storms accompanied by violent wind are common at this altitude from October to May. During the winter months the loose snow sweeps along the frozen surface in a manner suggesting sand storms. Observations in the spring of 1919 furnished an excellent illustration of the effect of wind action during the preceding winter. The trees and saplings at timber line on a broad ridge bordering the south side of a deep canyon almost invariably had their needles killed on the north side toward the canyon while on the south and sunny side they were uninjured (in lower altitudes injury of this kind is usually worse on the sunny side of the tree). Although the prevailing winds in this section are from the southwest, at this point the movement during the preceding winter was prevailingly north or northwest, coming up the canyon as demonstrated by a much shallower deposit of snow on the edge of the ridge bordering the canyon than a hundred feet back toward the south. The obvious explanation of the browning of the foliage is that the winds dry out the tissues excessively during the long winter period when soil moisture is not available to the roots on account of low temperature.

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[20] [Is it not possible also that the lack of cold temperatures to which the tree is accustomed in its natural habitat has interfered with its metabolism? Rigg, in a paper to appear in the next issue, quotes Lidforss as suggesting that the large sugar content of evergreen leaves in winter is probably due to the activation of a diastolic enzyme by low temperature. It would seem therefore that low temperature, aside from its influence on transpiration, plays an important part in the metabolic processes of the plant and could well account for the gradual decline of the Engelmann spruce seedlings transplanted to the Douglas fir type.—EDITOR.]

It seems fairly well established that the upper limit of Engelmann spruce *in tree form* is generally determined not by deficient heat supply for elaboration of plant food,[21] but by conditions affecting moisture supply as controlled by low soil temperature, high evaporation, abrasive action of wind and snow, and in some cases lack of soil. The above statement does not apply to the species in the trailing form as it occurs several hundred feet above the point where it ceases to exist as a tree. As we ascend to about 12,000 feet on the south and west sides of the peak, both the spruce and the bristle-cone pine become reduced to small bushes, and finally disappear entirely. In many instances this condition may be attributed to lack of soil, but occasionally we find between the boulders pockets of fairly deep soil protected from wind and apparently favorable to tree growth in all respects excepting temperature. Thus it appears that the *final* upper limit of both Engelmann spruce and bristle-cone pine is determined by temperature.

[21] [Summations of effective temperatures in the spruce type as compared with those in the alpine zone would help in further establishing or controverting this. Sampson (U. S. Dept. Agr. Bul. 700, 1918) indicates that effective temperature are of much importance.—Editor.]

Cork-Bark Fir.—Arizona cork-bark fir (*Abies arizonica*) is associated with Engelmann spruce throughout the latter's range until an altitude of about 11,000 feet is reached. Here the fir drops out on north slopes but continues a short distance on the more sunny exposures where protected from high winds. Its lower range is determined by the same conditions as those limiting the downward extension of Engelmann spruce. Its absence from the upper portion of the Engelmann spruce type is undoubtedly due to lack of heat for photosynthesis.

Bristle-cone Pine.—Bristle-cone pine (*Pinus aristata*) begins slightly higher than the Engelmann spruce, and persists to the same altitude as the latter. It rarely occurs on northerly exposures, due perhaps to the fact that on such sites it is shaded out by the spruce and fir, but it predominates on southerly exposures. Like the limber pine, it is able to maintain itself on wind-swept ridges and steep south slopes where its associates of other sites fail. Its lower altitudinal limit corresponds closely with the upper limit of limber pine, thus indicating a lower temperature and higher moisture requirement than the latter. Although it prevails on steep south slopes which suggest dry soil, it has been observed that the snow persists later on these sites than on limber pine sites and therefore it is quite likely that they enjoy more soil moisture than the latter.

In planting experiments in the yellow pine type during 1918, bristle-cone pine showed every indication of being perfectly adapted to its new habitat. This behavior may be due to the unusually heavy summer rainfall. It showed no evidence of injury from high temperature during the hottest periods of 1918 and 1919 when air temperatures mounted to as high as 89 degrees F. In the greenhouse it has under favorable moisture conditions been subjected to temperatures of 100° F. without evident injury.

The upper range on southerly exposures is apparently controlled by the same conditions as in the case of Engelmann spruce. On northerly aspects there is every indication of a limitation due to deficient heat supply. It is true that on such sites it is usually suppressed by the spruce, but the fact that it does not occur on northerly exposures above 11,000 feet even in openings indicates that it does not find favorable temperature conditions here.

CONCLUSIONS

The weight of evidence thus far accumulated in this study supports the hypothesis that the upper altitudinal range of all tree species in this region is determined by low temperature, and the lower altitudinal range by deficient moisture.

That low temperature, primarily as related to photo-synthesis, constitutes the upper control, seems established beyond serious doubt. This does not ignore the part played by winter killing resulting from excessive water loss at times when low soil temperature renders the moisture unavailable to the roots. Drought of this character may prove fatal to trees beyond the seedling stage, but in this region it will rarely affect seedlings in altitudes above the pinon-juniper type, for the reason that the ground usually remains deeply covered with snow during the period of dangerously low soil temperatures. If a species such as yellow pine should by any chance reach a height of 2 or 3 feet in the Engelmann spruce type, for instance (an attainment which winter conditions would permit) the probabilities are that it would eventually succumb to winter killing due to repeated dying back of the portion extending above the snow level. As a matter of fact, however, yellow pine or any other low altitude species does not occur in the Engelmann spruce type, even in the early seedling stage, for the reason that the temperature is too low for photosynthesis, to say nothing of germination.

When we attempt to decide which is the limiting factcor in the lower range the problem may become more complex. As explained above the effects of high temperature and low moisture are to a large extent inseparable. It is recognized that every species has its limit of high temperature endurance, but the evidence here deduced indicates that in actual practice the limit of drought endurance (considering resistance to water loss, ability to survive in a desiccated condition, and capacity for obtaining water) is reached before the temperature endurance is seriously taxed. For example, Engelmann spruce in this region reaches its extreme lower altitudinal limit at about 9,000 feet. If it is found by actual test that increased water supply will enable the spruce to grow in temperatures as high as those experienced in the yellow pine type at 7,500 feet, it is reasonable to conclude that the condition which prevents the spruce from descending below its present range is deficient moisture rather than excessive heat. This sort of test is being made with all but two or three of the native species. The results thus far have shown that all are able to withstand temperatures far in excess of those experienced at the lower limits of their present range. These tests are being continued with a view toward securing conclusive data.

Summary

1. Air temperature in the San Francisco Mountain region decreases rather uniformly with a rise in altitude excepting for local inversions in the minimum which occur between the yellow pine and the Douglas fir types, due to air drainage. The lowest absolute minima and the shortest frostless season occur in the yellow pine type, followed closely by the alpine type. The highest temperatures and greatest duration of high temperatures are found in the lowest altitudes. Maximum temperatures decrease uniformly from the lowest to the highest stations. The daily range is greatest in the lower altitudes, decreasing from about 50° F. in the pinon-juniper to about 20° F. in the Engelmann spruce. From the Engelmann spruce type to timber line there is a noticeable increase in range due to the exposed situation of the timber line station.

2. Precipitation increases rapidly with altitude up to the Douglas fir type. From the Douglas fir to the Engelmann spruce type it remains almost stationary, but at timber line there appears to be a substantial increase. On account of the great variability of precipitation a record of 2 years is not sufficient to establish a definite relation between the various forest types. All the types have about the same annual distribution which is roughly as follows: winter (Dec.-Mar.) 40 percent; spring (Apr.-May) 10 percent; summer (June-Aug.) 30 percent; autumn (Sept.-Nov.) 20 percent.

3. Wind movement is normally greatest in the higher altitudes, but this relation is not always indicated for the reason that some of the stations are located in the forest while others are in the open. The highest records are obtained at timber line which is entirely exposed, and the lowest in the spruce forest.

4. Evaporation records in this study show no constant relation to altitude, because wind movement and exposure to sunshine, two of the strongest factors influencing evaporation, vary at the different stations according to density of cover. The highest records obtained are in the pinon-juniper type, and the lowest in the Engelmann spruce type.

5. On the basis of origin there are several general soil types in this region. Those in the pinon-juniper type are derived from sandstone, limestone and basalt. In the yellow pine type local areas of limestone and sandstone occur near the lower limits but basaltic soils predominate over the type as a whole. Above the yellow pine type all the soils are derived from volcanic rocks.

Probably the most important soil character to be dealt with in this region is the capacity for absorbing and delivering moisture as determined by permeability, water holding capacity, and wilting coefficient. From this standpoint, the heavy clay soils common through the yellow pine type present the least favorable conditions for growth, particularly with respect to natural reproduction. Although these soils have a high water holding capacity, they also have a high wilting coefficient, and unless mixed with a large proportion of stone and gravel they are exceedingly impervious. High precipitation, low evaporation, and a high degree of permeability tend to create a large moisture supply in the Douglas fir and Engelmann spruce and Alpine types. At times of maximum vegetative activity, however, the available moisture supply in the Douglas fir and Engelmann spruce types may, on account of the heavy demands of the dense stands of trees, be reduced almost as low as in the forest types of relatively low precipitation and high evaporation.

Soil temperatures is of importance mainly through its indirect effects. When the soil temperature falls to 32° F. or even a few degrees above 32°, the soil moisture ceases to be available to plant roots. If this conditions persists continuously over long periods during which transpiration is favored by sunshine and wind the result may be fatal to a tree which is unable to endure extreme desiccation.

6. The data obtained in this study indicate that the upper limits of all the forest types are determined primarily by low temperature as related to photosynthesis, and that the lower limits are determined primarily by deficient moisture supply. Low soil temperature, by rendering the soil moisture unavailable to the roots, may under certain conditions as at timber line become the upper control; but, at least as far as reproduction is concerned, this is not believed to be a prevalent factor in this region, for the reason that in the high altitudes, the only places where long periods of continuously low soil temperature occur, transpiration in seedlings is reduced to a negligible quantity by a deep snow cover. Deficient moisture rather than high temperature is regarded as the lower control because observations supported by experimental data on nearly all of the species in this region indicate that when adequately supplied with moisture they are capable of enduring high temperatures far in excess of those which occur at the lower limits of their natural range.

NOTE: The foregoing article was originally prepared a year and a-half ago. Meteorological records were continued up to December 31, 1920, and investigations on other phases of the subject are still in progress as the article goes to press. While subsequent data have not appreciably modified the conclusions here presented they will permit more exhaustive treatment in a forthcoming publication.—AUTHOR.